

A Native Besieged: Effects of Nonnative Frugivores and Ground Vegetation on Seed Removal in a Highly Endangered Hawaiian Shrub, *Delissea rhytidosperma* (Campanulaceae)¹

Tracy L. Erwin² and Truman P. Young^{2,3}

Abstract: Nonnative species can have serious negative effects on regeneration and restoration of rare plant taxa, particularly in insular ecosystems. An endangered Hawaiian shrub, *Delissea rhytidosperma* (Campanulaceae), produces fruits and viable seeds, but no regeneration has been observed in the wild. We used cages and vegetation removal to explore direct and indirect effects of three groups of nonnative species on suspected seed predation of this endangered plant: a mat-forming grass (*Oplismenus hirtellus*), rats (*Rattus* spp.), and invertebrates. Substantial seed removal occurred in all treatments. Both rat exclusion and clearing of nonnative vegetation had strong significant negative effects on seed removal. Highest removal rates occurred with rats not excluded and vegetation present, and lowest removal occurred when rats were excluded and vegetation cleared. Without rat exclusions, 100% of seeds were removed within 15 days. Even when protected from rats, most seeds were removed by smaller herbivores, unless ground vegetation was cleared. Vegetation appears to harbor invertebrates that eat seeds, including nonnative slugs. These results revealed that different nonnative species combine to greatly increase rates of seed removal in endangered *D. rhytidosperma*.

ISLANDS MAY BE particularly disharmonic environments where herbivory and predation by nonnative animals can have strong negative impacts on the survival and recruitment of sensitive native plant taxa (Carlquist 1972, Vitousek et al. 1995, Athens et al. 2002, Brueggemann et al. 2002, Drake et al. 2002). In Hawai'i, these nonnative species include both animals that eat native seeds and seedlings, and plants that compete with natives as well as affecting the foraging behavior of destructive animals. Most research investigating

the effects of rodents on island ecosystems has focused on predation of native fauna, particularly birds and small reptiles (Atkinson 1977, Scott et al. 1988, Athens et al. 2002, Campbell and Atkinson 2002). However, rodents can have large effects on plant recruitment as well (Andersen 1989, Asquith et al. 1997, Hulme 1998).

The negative effects of rodents on plants have been well documented in many continental ecosystems where rodents are native. Such studies typically use rodent exclosures to tease apart the effects of larger fruit or seed predators from those of smaller predators (primarily invertebrates). Rats eat flowers and fruits on plants, fallen fruit, seeds, and seedlings and can greatly reduce seed available for germination (Janzen 1971, Schupp 1988, deMattia et al. 2004). Postdispersal seed predation by rodents can be great enough to affect population dynamics and limit population viability (Andersen 1989, Asquith et al. 1997, Hulme 1998).

The limited research that has been conducted on the effects of nonnative rodents

¹ Funding for this research came from the University of California and the Pacific Rim Research Program. Manuscript accepted 10 February 2009.

² Department of Plant Sciences, University of California, Davis, California 95616.

³ Corresponding author (e-mail: tpyoung@ucdavis.edu).

on island flora has also shown that they can reduce regeneration and restoration of plants and affect plant community dynamics (Vitousek et al. 1995, Campbell and Atkinson 2002). Nonnative rats in the Canary Islands greatly reduced seed survival of the most common forest tree, *Ilex canariensis* (Salvande et al. 2006). Of 16 tree species studied on islands in New Zealand, 11 showed evidence of depressed recruitment due to seed and fruit predation by nonnative rodents (Campbell and Atkinson 2002). It has been suggested that on some New Zealand islands rodents are responsible for local plant extinctions (Towns and Broome 2003).

In Hawai'i, rodents and many nonnative invertebrates are suspected of reducing plant recruitment by acting as seed predators before or after seeds are dispersed (Loope et al. 1988, Drake 1998, Cox 1999, Traveset and Richardson 2006). In addition, nonnative plant species strongly compete with native Hawaiian vegetation, and their presence can alter community dynamics and affect microclimates (Vitousek et al. 1995). Novel predators and changes in plant composition may work synergistically to reduce plant recruitment in native species that are sensitive to these invasive species.

Invertebrate species can also reduce plant recruitment (Hulme 1997). The presence of vegetation cover may affect the distribution and activity of these potential fruit removal species, increasing the risk of seed loss (Root 1973, Rauscher 1981, Bergelson 1990, Gurevitch et al. 2000, Rand 2004). Complex vegetation structure may improve seed dispersal by trapping seeds (Schupp et al. 1989, Russell and Schupp 1998, Bullock and Moy 2004) or making fruits and seeds less apparent to herbivores. However, these environments can also harbor invertebrate seed predators and herbivores such as snails, slugs, beetles, and bugs because vegetation provides food and safety (Newell 1967, Collins and Uno 1985, Kjellson 1985, Crawley 1997). Nonnative vegetation can also competitively exclude native plant seedlings (Loope et al. 2004).

There has been little research on the direct effect of invertebrate predation on Hawaiian

fruits or seeds, although it is assumed to be a common occurrence (Howarth 1985). Recently, attention on Maui has focused on the widespread seed predation by the bruchid beetle, *Specularis impressithorax*, on the most common native dry-forest tree, *Erythrina sandwicensis*. In wetter forest in Hawai'i, nonnative slugs eat seedlings of many native plants (Sailor 2002), and this has recently been quantified for some of them, particularly species in the family Campanulaceae and Asteraceae (Joe and Daehler 2008).

In highly invaded ecosystems, like those in Hawai'i, multiple guilds of invasive species may combine to threaten native species (e.g., Freed et al. 2008). However, rarely are multiple threats simultaneously studied for a particular species.

There are many rare plant species in Hawai'i that are experiencing poorly understood recruitment bottlenecks resulting in little or no population regeneration (Erwin 2007). *Delissea rhytidosperma* is one such species where no natural recruitment had ever been observed when the species was still extant in the wild. The remnant individuals flowered, produced fruit and viable seed, but no seedlings had ever been found (Dave Bender and Ken Wood, National Tropical Botanical Garden [NTBG], pers. comm.). Now this species is extinct in the wild. Considering this history, the recruitment bottleneck is most likely to be one of the following: pre- or postdispersal seed predation, loss of dispersal agent, lack of appropriate germination "safe sites," early seedling predation, or competition at the seedling stage. We examined the potential loss of seed to predators. The fruits of *D. rhytidosperma* are fleshy and lipid-rich, and there is an abundance of potential frugivores in the Hawaiian rain forest. Our study measured fruit removal, not seed predation directly, because it is very difficult to be certain of the fate of removed seeds.

This study sought to answer the following questions: (1) Are nonnative rodents and invertebrates responsible for significant removal of *Delissea rhytidosperma* seeds? (2) Does the presence of nonnative ground vegetation have an effect on seed removal?

MATERIALS AND METHODS

Species and Study Site

The genus *Delissea* (Campanulaceae) is among the most threatened of Hawai'i's endemic genera. There are 10 known species, of which six are thought to be extinct in the wild (U.S. Fish and Wildlife Service [USFWS] 2000, 2002). *Delissea rhytidosperra* is endemic to Kaua'i and was historically known on the island from one primary locality. It once occurred between the elevations of 120 and 915 m (USFWS 1995) in diverse mesic forests and *Acacia koa*-dominated lowland dry forests (Wagner et al. 1999a). Currently, this species is considered extinct in the wild (Ken Wood, NTBG, pers. comm.; USFWS 2007), although there are restoration outplantings (see later in this section). *Delissea rhytidosperra* is a federally listed endangered species (USFWS 1994).

Delissea rhytidosperra is a small shrub up to 2.5 m tall (Wagner et al. 1999a). Plants begin flowering in spring, and fruit begins to ripen in mid- to late summer (D. Bender, NTBG, pers. comm.). Fruits are berries 7–12 mm in diameter, which when ripe have red-black skin, lipid-rich pulp, and are probably bird-dispersed (Wagner et al. 1999b, Lammers 2005). Each fruit contains approximately 50–100 seeds, 0.7–1.0 mm in diameter. Seeds manually removed from fruits germinate between 3 weeks and 6 months after planting in nursery settings (Yoshinaga 2002).

Over 200 individuals of *D. rhytidosperra* have been outplanted at a 400 ha managed restoration site, Limahuli Preserve, located on the north shore of Kaua'i, owned and managed by the National Tropical Botanical Garden. There is no "natural" regeneration at this restoration site. This research was carried out at the restoration population in the 245 ha lower section of the Preserve. The area is an alien-dominated forest with several small remnant patches of native vegetation. There are several well-established woody invasive plants that dramatically alter the native forest, such as common guava (*Psidium guajava*), octopus tree (*Schefflera actinophylla*), and Christmas berry (*Schinus terebinthifolius*). In

addition, nonnative mat-forming grasses are abundant throughout the study site, in particular basket grass (*Oplismenus hirtellus*). The native understory vegetation consists primarily of scattered ferns, has no mat-forming grasses, and is much more open (has more bare ground) than the forest floor community invaded by mat-forming grasses.

It is believed that threats to *D. rhytidosperra* include predation and habitat degradation by deer, pigs, and goats, and herbivory by rats and introduced slugs (USFWS 2002, 2007). Fire and competition with the alien plants also threaten this species. Additional potential threats include a risk of extinction from naturally occurring events, such as landslides or hurricanes (USFWS 1995, 2000).

Field Experiments

The objective of this study was to quantify fruit removal of *D. rhytidosperra* and to assess the effects of different animals and ground vegetation on fruit removal. We established three 15 by 15 m plots in the vicinity of the restoration population of *D. rhytidosperra*. One plot was located within this population, one was located 10 m from the nearest adult, and the third was located 20 m from the nearest adult, as a check on (but not a formal test of) distance effects. All three plots were at the same elevation with similar microhabitat.

Within each plot was a 2 by 2 randomized design with two crossed treatments: rat exclusion (caged/not caged), and vegetation removal (cleared/not cleared). There were 10 replicates for each of the four treatment combinations in each plot in a 15 by 15 m grid, separated from each other by at least 0.5 m.

Two *D. rhytidosperra* fruits were placed on the ground in the center of each of the 120 treatment sites on 22 July 2004. Because this plant is rare and very few fruits were available, only two fruits were used per site. Fruits were collected from 20 different fruiting adult individuals from the population within the same week before the beginning of the experiment. All fruits were inspected for insect and fungal damage, and these 5% were excluded. Fruits from different individuals were com-

bined and then randomly assigned to the four experimental treatments. Ripe fruits do drop off of this species and lie on the ground around the adult plant. Placing these fruits on the ground was meant to approximate both this passive dropping and the dispersal of seeds by a bird disperser. The form of the seed packaging was ripe fruit, rather than feces, but we hoped nonetheless to get a sense of the removal rates of these seeds after reaching the ground.

For vertebrate-proof enclosures we used 10 by 61 cm cylinders composed of 2 cm polyethylene diamond mesh netting. The enclosures were supported with bamboo stakes. The bottom edge of the enclosure was buried 5 cm below ground and held with metal stakes to prevent any openings. The tops of the enclosures were held closed by plastic cable ties. The 2 cm mesh of these cages was not large enough to allow access to the enclosure by larger rats or birds, or any larger vertebrate. However, this mesh size could allow entry by mice or perhaps smaller rats (Douglas Kelt, University of California, Davis, pers. comm.) and invertebrates. In practice, we never saw any vertebrates or rodent droppings in any of these 60 cages visited many times throughout the experiment.

In the vegetation removal treatments, 1 m diameter plots were cleared of all above-

ground plant material to bare soil, and the fruits were placed in the center of the cleared circle. For the control treatments, the fruits were placed on the vegetation in the center of the 1 m plot. Before clearing, the vegetation in the plots was 100% cover by the non-native mat-forming grass *Oplismenus hirtellus*.

Fruits were censused on days 2, 3, 4, 5, 7, 9, 11, 16, and 20. The proportion of the fruits that remained was recorded to the nearest quarter-piece of fruit. Because seeds are distributed evenly throughout fruits, a record of 25% removal of fruit suggests 25% removal of seeds. Therefore, hereafter we will report seed removal. The presence of any invertebrates on the fruits or birds on the ground near the fruits was recorded but not quantified.

In all analyses, values were averaged over the 10 replicates of each treatment in each of the three plots, and these plot means were used in the analysis. Because these analyses looked at seed removal over time for the different treatments, we used repeated measures analysis of variance (ANOVA) to test equality of group means. This technique provides an adjusted *F*-value. Because all of the seed exposed to vertebrates was removed (the lower two curves in Figure 1), we calculated the mean number of days it took for half of the seed to be taken for the vegetation treatments

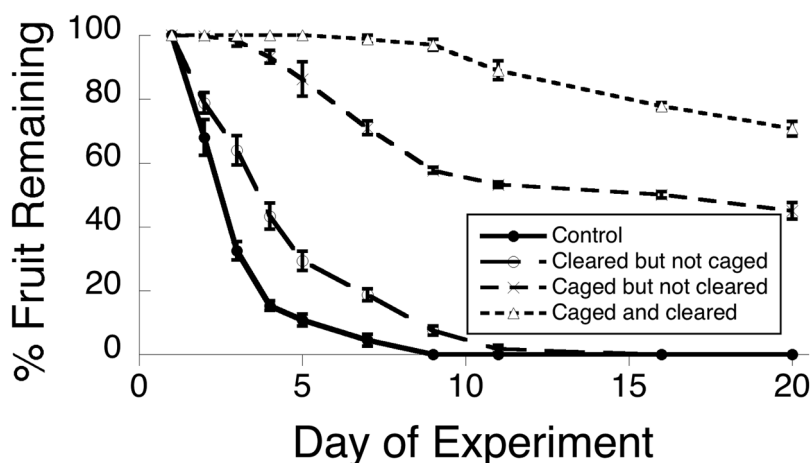


FIGURE 1. Seed removal through time in each of the four treatments. Bars are 1 standard error, based on means from the three replicate plots.

across all distances and analyzed these data with a two-way ANOVA. For the fruits used in this analysis (not protected by an enclosure), more than 80% of the observations of seed removed occurred in the first 5 days of the experiment, when data were collected every day. We performed a two-way ANOVA with interaction on the seed remaining using plot and vegetation removal as factors. All data sets tested with ANOVA met the appropriate assumptions. At the end of the experiment (day 20), for all treatments we tested for treatment effect on the amount of seed remaining. Because the data could not be transformed to meet assumptions of equal variance, we used a Wilcoxon/Kruskal-Wallis Test (rank sums) to compare just the vertebrate exclusion treatments for seed remaining.

RESULTS

Although we found no evidence of mice (*Mus musculus*) at the study site, nonnative slugs and (nonnative) carabid beetles were found eating fruits both within and outside the rat enclosures. These species were not identified at finer taxonomic levels. Although this was not quantified, there did not appear to be differences between the number of invertebrates observed eating fruit inside and outside the enclosures. Neither native nor nonnative birds were ever observed at the fruit piles.

For all of the traits below, there are no significant differences among the three plots (all *P* values > .50), which behaved very similarly (note the very small error bars in Figure 1).

Rate of Seed Removal

Both vertebrate exclusion and vegetation clearing significantly reduced the amount of seed removal over time (Table 1). The significant interactions with Time in this repeated measures ANOVA revealed that temporal patterns of removal differed among treatments. The seeds that were not protected by an enclosure were quickly and completely removed (Figure 1). When the experiment ended on day 20, many seeds remained in the vertebrate enclosure treatments, especially in cleared treatments.

TABLE 1

Results of Repeated Measures ANOVA on Effects of Plot, Vegetation Removal, Caging, and Time on Percentage of Seeds Remaining

Source	df	F ratio	P
Plot	2	0.254	.78
Vegetation	1	63.1	<.0001
Enclosure	1	824.7	<.0001
Vegetation * Enclosure	1	1.83	.18
Time * Vegetation	9	11.15	<.0001
Time * Enclosure	9	117.0	<.0001
Time * Vegetation * Enclosure	9	8.06	<.0001

TABLE 2

Results of ANOVA on Effects of Plot Location (Distance from Adult Stand) and Vegetation Removal on Rate of Seed Removal (Days to Half Seeds Removed) and Seeds Remaining at End of Experiment, for Uncaged Treatments

Source	df	F ratio	P
Rate			
Plot	2	0.11	.90
Vegetation	1	6.07	.017
Plot * Vegetation	2	0.56	.57
Seeds remaining			
Plot	2	0.005	.99
Vegetation	1	4.72	.032
Plot * Vegetation	2	0.13	.88

The presence of vegetation significantly increased the amount of seed removal across all three plots (Table 2 [Rate], Figure 1). The mean number of days to removal of half of the seeds was 3.9 ± 2.1 (S.E.) days in the two vegetation-removal treatments and 2.7 ± 0.7 days in the two treatments with vegetation left intact.

Total Seed Removal after 20 Days

There were no significant differences in total seed removal among the three replicate plots (Table 2 [Seeds Remaining]). There were significant negative effects of vertebrate exclusion and vegetation removal on total seed removal. Although 58% of seeds that were protected by cages still remained after the end of the experiment (day 20), all un-

protected seeds were removed by day 15 ($\chi^2 = 100.5$, $P < .0001$) (Figure 1). For seeds protected by exclosures, the absence of vegetation resulted in significantly more seeds remaining (72% versus 45%) (Table 2 [Seeds Remaining]). There were no significant interactions among the three factors (plot, exclosure, vegetation) for total seed removal (all $P > .20$).

DISCUSSION

We have evidence that three different guilds of invasive species have direct or indirect effects on the removal of seeds of the endangered Hawaiian shrub species *Delissea rhytidosperra*. Specifically, our experiments revealed three main patterns: (1) the exclusion of nonnative rats significantly decreased seed removal, (2) the removal of nonnative vegetation significantly decreased seed removal, and (3) considerable seeds were removed even when protected from rats and were more quickly removed when nonnative vegetation was present.

Seed Removal by Rats

All of the native forest birds potentially present at the site are insectivorous (*Hemignathus virens*, *Himatione sanguinea*, *Chasiempis sandwicensis*). There are several nonnative frugivorous birds present at the study site (*Acridotheres tristis*, *Mimus polyglottos*, *Zosterops japonicus*) that may eat the fruit of *D. rhytidosperra* while still on the adult shrub and may serve as seed dispersers. However, these particular avian frugivores forage primarily in the subcanopy or the understory (Mountain-spring and Scott 1985, Scott et al. 1986) and are not likely to collect fruits from the ground. Typically, most bird frugivores in the tropics do not forage on the ground unless there is a shortage of fruit or other foods in safer regions of the canopy or understory (Smythe 1970). In addition, birds were never observed feeding at the study stations over many days of visitation.

The only other large herbivore known to occur at this site is rats, most likely the black rat (*Rattus rattus*) and/or the Polynesian rat

(*R. exulans*), which are thought to be the species responsible for rodent fruit and seed predation in other wild plant populations (Stone and Loope 1987, Lindsey et al. 1999, Nelson et al. 2002). We therefore think that it is likely that nonnative rats were the main species responsible for the removal of uncaged seeds.

Fruit or seed removal does not necessarily demonstrate the death of seeds (Forget 1991, VanderWall et al. 2005). Some of the seed moved or cached by small rodents could potentially escape predation and have the opportunity to germinate (Terborgh and Wright 1994, Hoch and Adler 1997, Brewer and Rejmanek 1999). This may even be true for slugs (see discussion in the next section). However, the effect of small rodents on plant recruitment has often been shown to be negative (Vandermeer et al. 1979, Howe and Smallwood 1982, Crawley 1992, Wenny 2000). Typically, the smaller the herbivore, the less likely the seed is to survive (deMattia et al. 2004). There was no evidence at our study site that seeds survive removal (no germinated seedlings were observed anywhere in the vicinity of the site during the study).

Our results provide experimental evidence that rats may contribute considerably to *Delissea* seed predation. Rat exclusion produced the lowest seed removal rate and overall proportion of seeds removed (Figure 1). Without rat exclusion all seeds were removed by day 15. Because seeds typically germinate between 3 weeks and 6 months of planting, such rapid removal would not allow enough time for any of the seeds to germinate in situ. This study suggests that rats may contribute to a loss in recruitment success for *Delissea rhytidosperra*. Other studies have come to similar conclusions about rats and plants both in Hawai'i (Cuddihy and Stone 1990) and elsewhere (Janzen 1971, Crawley 1989a,b, Baskin and Baskin 1998, Blaney and Kotanen 2001, Plucinski and Hunter 2001).

Nonnative Vegetation and Invertebrate Herbivores

Seed removal within rat exclusion cages could be attributable to invertebrate herbivores,

mice (*Mus musculus*), or perhaps immature *Rattus* spp. We found no evidence of mice at our study site. To our knowledge, nothing is known about *M. musculus* as a fruit/seed predator in Hawai'i, although there is evidence that indicates that over half of their diet is insect material and that they are more common in dry forest than in wet forest (Amarasekare 1994). On the other hand, we recorded both nonnative slugs and (nonnative) carabid beetles eating fruits, but not native invertebrates, in both caged and uncaged treatments. However, it is always possible that some of the seed removal we attribute to nonnative invertebrates here could be due to nonnative *M. musculus* (or young *Rattus* sp.).

At the study site, nonnative slugs are common and are likely contributing to seed removal. There are no native slugs in Hawai'i, although there is a rich fauna of native snails (Cowie 1998). At least 12 species of nonnative slugs are now established in Hawai'i, some at high elevations where most intact native forest remains (Joe and Daehler 2008). The plant family Campanulaceae appears to be especially attractive to slugs in Hawai'i (Sailor 2002).

A study on the effect of slug herbivory on Hawaiian plants at the seedling stage found that slugs show preferences for certain species of plants and that they reduce plant growth and increase seedling mortality (Joe and Daehler 2008). It is likely that slugs can have just as severe an effect on seeds as on seedlings. To our knowledge, no previous research has been conducted on invertebrate predation of fruits and seeds in Hawai'i.

Independent of caging treatment, the presence of the nonnative mat-forming grass also increased seed removal. We suspect that this was due to the increased incidence of invertebrates in vegetated areas in the study site. Vegetation harbors invertebrate herbivores such as snails, slugs, beetles, and bugs because it provides food and safety from predators and desiccation (Newell 1967, Grime and Blythe 1969, Collins and Uno 1985, Kjellson 1985, Rathcke 1985, Bergelson 1990, Crawley 1997).

At the study site, the canopy is more open

than that of most native forests and is dominated by nonnative trees. Ferns are the most common understory plant in a healthy, intact native Hawaiian forest (Carlquist 1972) and provide a more open understory with areas of exposed soil. At the study site, however, the understory cover is nearly 100% nonnative basket grass (*Oplismenus hirtellus*), a dense mat-forming grass. Such dense vegetation is likely to change the microenvironment near the soil and thus is likely to have an effect on the invertebrate community and may also provide cover for rodents. This dense grass species may also be a strong competitor of native trees at the seedling stage, but that was not the focus of this research. Our results suggest that this grass harbors smaller (invertebrate) frugivores and thus its presence contributes to the removal of fruits and seeds of susceptible native plants.

CONCLUSIONS

These results suggest that three different nonnative taxa combine to greatly increase postdispersal seed removal of *Delissea rhytidosperra*. Both nonnative rats and smaller herbivores (such as nonnative slugs) remove most seeds within a few weeks of dispersal. In addition, seed removal by invertebrates seems to be facilitated by a nonnative mat-forming grass. These same species may also limit recruitment at other life stages of *D. rhytidosperra*, such as germination sites and seedling establishment. Similar experiments on planted seedlings would be helpful.

Although we present data here for nonnative species contributing to fruit and seed removal of *D. rhytidosperra*, we are not asserting that this seed removal is the only, or even the most important, factor limiting recruitment of this endangered species. Other threats are likely to include fire, competition with the alien plants, and predation and habitat degradation by deer, pigs, and goats (USFWS 2002, 2007). However, our results provide information that we think will be useful for rescue strategies for this species. Non-nursery restoration of *D. rhytidosperra*, and similar species, should consider preventing access of rats and slugs to sown ripe fruits

and seeds. In addition, removal of nonnative vegetation around fruiting trees is likely to reduce fruit removal and seed loss and promote natural regeneration.

ACKNOWLEDGMENTS

Cooperation with the National Tropical Botanical Garden made this project possible. We would like to thank David Burney, Ken Wood, and David Bender from the National Tropical Botanical Garden for help with support and logistics. Rick Karban and Valerie Eviner helped with analysis and writing of the manuscript. Two anonymous reviewers greatly improved the manuscript.

Literature Cited

- Amarasekare, P. 1994. Ecology of introduced small mammals on western Mauna Kea, Hawaii. *J. Mammal.* 75:24–38.
- Andersen, A. N. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia (Berl.)* 81:310–315.
- Asquith, N. M., J. S. Wright, and M. J. Clauss. 1997. Does mammal community composition control recruitment in neotropical forest? Evidence from Panama. *Ecology* 78:941–946.
- Athens, J. S., H. D. Tuggle, J. V. Ward, and R. J. Welch. 2002. Avifaunal extinction, vegetation change, and Polynesian impacts in prehistoric Hawaii. *Archaeol. Oceania* 37:57–78.
- Atkinson, I. A. E. 1977. A reassessment of factors, particularly *Rattus rattus* L., that influenced the decline of endemic forest birds in the Hawaiian Islands. *Pac. Sci.* 31:109–133.
- Baskin, C. C., and J. M. Baskin. 1998. Seeds: Ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego.
- Bergelson, J. 1990. Spatial patterning in plants: Opposing effects of herbivory and competition. *J. Ecol.* 78:937–948.
- Blaney, C. S., and P. M. Kotanen. 2001. Post-dispersal losses to seed predators: An experimental comparison of native and exotic old field plants. *Can. J. Botany* 79:284–292.
- Brewer, S. W., and M. Rejmanek. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *J. Veg. Sci.* 10:165–177.
- Bruegmann, M. M., V. Caraway, and M. Maunder. 2002. A safety net for Hawaii's rarest plants. *Endang. Spec. Bull.* 27:8–11.
- Bullock, J. M., and I. L. Moy. 2004. Plants as seed traps: Inter-specific interference with dispersal. *Acta Oecol.* 25:35–41.
- Campbell, D. J., and I. A. E. Atkinson. 2002. Depression of tree recruitment by the Pacific rat (*Rattus exulans* Peale) on New Zealand's northern offshore islands. *Biol. Conserv.* 107:19–35.
- Carlquist, S. 1972. Island biology. Columbia University Press, New York.
- Collins, S. L., and G. E. Uno. 1985. Seed predation, seed dispersal and disturbance in grasslands: A comment. *Am. Nat.* 125:866–872.
- Cowie, R. 1998. Patterns of introduction of non-indigenous non-marine snails and slugs in the Hawaiian Islands. *Biodiv. Conserv.* 7:349–368.
- Cox, G. H. 1999. Alien species in North America and Hawaii: Impacts on natural ecosystems. Island Press, Washington, D.C.
- Crawley, M. J. 1989a. Insect herbivores and plant population dynamics. *Annu. Rev. Entomol.* 34:531–64.
- . 1989b. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. Pages 45–71 in E. A. Bernays, ed. *Insect-plant interactions*. Vol. 1. CRC Press, Boca Raton, Florida.
- . 1992. Seed predators and population dynamics. Pages 157–191 in M. Fenner, ed. *Seeds: The ecology of regeneration in plant communities*. C.A.B. International, Oxon, United Kingdom.
- . 1997. Plant-herbivore dynamics. Pages 401–474 in M. J. Crawley, ed. *Plant ecology*. Blackwell Science, Oxford.
- Cuddihy, L. W., and C. P. Stone. 1990. Alteration of native Hawaiian vegetation: Effects of humans, their activities and in-

- roductions. University of Hawai'i Press, Honolulu.
- deMattia, E. A., L. M. Curran, and B. J. Rathcke. 2004. Effects of small rodents and large mammals on neotropical seeds. *Ecology* 85:2161–2170.
- Drake, D. R. 1998. Relationships among the seed rain, seed bank, and vegetation of a Hawaiian forest. *J. Veg. Sci.* 9:103–112.
- Drake, D. R., C. P. H. Mulder, D. R. Towns, and C. H. Daugherty. 2002. The biology of insularity: An introduction. *J. Biogeogr.* 29:563–569.
- Erwin, T. L. 2007. Recruitment limitation in endangered Hawaiian plants. M.S. thesis, University of California, Davis.
- Forget, P. M. 1991. Scatterhoarding of *Astrocaryum paramaca* by *Proechimys* in French Guiana: Comparison with *Myoprocta exilis*. *Trop. Ecol.* 32:155–1647.
- Freed, L. A., R. L. Cann, and G. R. Bodner. 2008. Incipient extinction of a major population of the Hawaii akepa owing to introduced species. *Evol. Ecol. Res.* 10:931–965.
- Grime, J. P., and G. M. Blythe. 1969. An investigation of the relationship between snails and vegetation at the Winnats Pass. *J. Ecol.* 57:45–66.
- Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: A meta-analysis of field experiments. *Am. Nat.* 155:435–453.
- Hoch, G. A., and G. H. Adler. 1997. Removal of black palm (*Astrocaryum standleyanum*) seed by spiny rats (*Proechimys semispinosus*). *J. Trop. Ecol.* 13:51–58.
- Howarth, F. G. 1985. Impacts of alien land arthropods and mollusks on native plants and animals in Hawaii. Pages 149–179 in C. P. Stone and J. M. Scott, eds. *Hawaii's terrestrial ecosystems: Preservation and management*. University of Hawai'i Cooperative National Park Resources Study Unit, Honolulu.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13:201–228.
- Hulme, P. E. 1997. Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. *Oecologia (Berl.)* 111:91–98.
- . 1998. Post-dispersal seed predation: Consequences for plant demography and evolution. *Perspect. Plant Ecol. Evol. Syst.* 1:32–46.
- Janzen, D. H. 1971. Seed predation by animals. *Annu. Rev. Ecol. Syst.* 2:465–492.
- Joe, S. M., and C. C. Daehler. 2008. Invasive slugs as under-appreciated obstacles to rare plant restoration: Evidence from the Hawaiian Islands. *Biol. Invas.* 10:245–255.
- Kjellson, G. 1985. Seed fate in a population of *Carex pilulifera* L. II. Seed predation and its consequences for dispersal and seed bank. *Oecologia (Berl.)* 67:424–429.
- Lammers, T. G. 2005. Revision of *Delissea* (Campanulaceae-Lobelioideae). *Syst. Bot. Monogr.* 73:1–75.
- Lindsey, G. D., S. M. Mosher, S. G. Fancy, and T. D. Smucker. 1999. Population structure and movements of introduced rats in a Hawaiian rainforest. *Pac. Conserv. Biol.* 5:94–102.
- Loope, L. L., O. Hamann, and C. P. Stone. 1988. Comparative conservation biology of oceanic archipelagoes: Hawaii and the Galapagos. *BioScience* 38:272–282.
- Loope, L. L., F. Starr, and K. Starr. 2004. Protecting endangered plant species from displacement by invasive plants on Maui, Hawaii. *Weed Technol.* 18:1472–1474.
- Mountainspring, S., and J. M. Scott. 1985. Interspecific competition among Hawaiian forest birds. *Ecol. Monogr.* 55:219–239.
- Nelson, J. T., B. L. Woodworth, S. G. Fancy, G. D. Lindsey, and E. J. Tweed. 2002. Effectiveness of rodent control and monitoring techniques for a montane rainforest. *Wildl. Soc. Bull.* 30:82–92.
- Newell, P. F. 1967. Mollusca. Pages 412–433 in A. F. Burges and R. Raw, eds. *Soil biology*. Academic Press, London.
- Plucinski, K. E., and M. L. Hunter. 2001. Spatial and temporal patterns of seed predation on three tree species in an oak-pine forest. *Ecography* 24:309–317.
- Rand, T. A. 2004. Effects of environmental context on the susceptibility of *Atriplex patula* to attack by herbivorous beetles. *Oecologia (Berl.)* 121:39–46.

- Rathcke, B. 1985. Slugs as generalist herbivores: Test of three hypotheses on plant choice. *Ecology* 66:828–836.
- Rausher, M. D. 1981. The effect of native vegetation on the susceptibility of *Aristolochia reticulata* (Aristolochiaceae) to herbivore attack. *Ecology* 62:1187–1195.
- Root, R. B. 1973. Organization of a plant–arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43:95–124.
- Russell, S. K., and E. W. Schupp. 1998. Effects of microhabitat patchiness on patterns of seed dispersal and seed predation of *Cercocarpus ledifolius* (Rosaceae). *Oikos* 81:434–443.
- Sailor, D. 2002. Slug barrier trail for *Solanum sandwicense*, *Urera kaalae* and *Schiedea kaalae*. The Nature Conservancy, Honolulu, Hawai'i.
- Salvande, M., M. Mulet, and L. A. G. Gonzalez. 2006. *Ilex canariensis* Poir. (Aquifoliaceae) post-dispersal seed predation in the Canary Islands. *Plant Ecol.* 187:143–151.
- Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51:71–78.
- Schupp, E. W., H. F. Howe, C. K. Augspurger, and D. J. Levey. 1989. Arrival and survival in tropical treefall gaps. *Ecology* 70:562–564.
- Scott, J. M., C. B. Kepler, C. van Riper III, and S. I. Fefer. 1988. Conservation of Hawaii's vanishing avifauna. *BioScience* 38:238–253.
- Scott, J. M., S. Mountspring, F. L. Ramsey, and C. B. Kepler. 1986. Forest bird communities of the Hawaiian Islands: Their dynamics, ecology, and conservation. *Stud. Avian Biol.* 9.
- Smythe, N. 1970. Relationships between fruiting season and seed dispersal method in a neotropical forest. *Am. Nat.* 140:25–35.
- Stone, C. P., and L. L. Loope. 1987. Reducing impacts of introduced species in Hawaii: What is being done, what needs doing, and the role of national parks. *Environ. Conserv.* 14:245–258.
- Terborgh, J., and S. J. Wright. 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. *Ecology* 75:1829–1833.
- Towns, D. R., and K. G. Broome. 2003. From small Maria to massive Campbell: Forty years of rat eradications from New Zealand islands. *N. Z. J. Zool.* 30:377–408.
- Traveset, A., and D. M. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol. Evol.* 21:208–216.
- U.S. Fish and Wildlife Service. 1994. Determination of endangered or threatened status for 24 plants from the island of Kauai, HI. *Fed. Regis.* 59, 38:9304–9329.
- . 1995. Recovery plan for the Kauai plant cluster. Portland, Oregon.
- . 2000. Determinations of whether designation of critical habitat is prudent for 81 plants and proposed designations for 76 plants from the islands of Kauai and Niihau, Hawaii [Proposed Rule]. *Fed. Regis.* 65, 216:66807–66885.
- . 2002. Revised determinations of prudence and proposed designations of critical habitat for plant species from the islands of Kauai and Niihau, Hawaii. *Fed. Regis.* 67, 18:3940–4098.
- . 2007. *Delissea rhytidosperra* 5-year review: Summary and evaluation. Pacific Island Fish and Wildlife Office, Honolulu, Hawai'i.
- Vandermeer, J. H., J. Stout, and S. Risch. 1979. Seed dispersal of a common Costa Rican rain forest palm (*Welfia georgii*). *Trop. Ecol.* 20:17–26.
- VanderWall, S. B., K. M. Kuhn, and M. J. Beck. 2005. Seed removal, seed predation, and secondary dispersal. *Ecology* 86:801–806.
- Vitousek, P. M., L. L. Loope, and H. Andersen, eds. 1995. *Islands: Biological diversity and ecosystem function*. Springer-Verlag, Berlin.
- Wagner, W. L., M. M. Brueggmann, D. R. Herbst, and J. Q. C. Lau. 1999a. Hawaiian vascular plants at risk. *Bishop Mus. Occas. Pap.* 60:1–64.
- Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999b. *Manual of the flowering plants of Hawai'i*. Rev. ed. University of

- Hawai'i Press and Bishop Museum Press, Honolulu.
- Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecol. Monogr.* 70:331–351.
- Yoshinaga, A. 2002. Seed storage characteristics of Hawaiian species. University of Hawai'i, Honolulu, Hawai'i 96848. <http://www.hawaii.edu/scb/seed/seedtabl.html> (accessed: January 2007).

